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SUN AND SHADE MEDIATE COMPETITION IN THE BARNACLES *CHTHAMALUS* AND *SEMIBALANUS*: A FIELD EXPERIMENT

DAVID S. WETHEY

Department of Biology and Marine Science Program, University of South Carolina, Columbia, South Carolina, 29208

ABSTRACT

The barnacles *Chthamalus fragilis* and *Semibalanus balanoides* compete for space in the high intertidal zone in southern New England. *Chthamalus* settles throughout the intertidal and persists in the absence of competition with *Semibalanus*. *Semibalanus* also settles throughout the intertidal but is usually eliminated from the high intertidal zone by heat and/or desiccation. In a field experiment in the high intertidal zone, *Semibalanus* survived the high summer temperatures and overgrew *Chthamalus* under an opaque roof. Under a transparent roof and in control areas with no roof, *Semibalanus* died in mid summer, and *Chthamalus* persisted. Hence the intensity of interspecific competition is mediated by physical stress which primarily affects the dominant competitor.

INTRODUCTION

A paradigm of intertidal zonation is that local upper shore limits are set by physical stress (heat, desiccation) and local lower shore limits are set by biotic interactions (predation, competition) (*e.g.*, Connell, 1961, 1972, but see also Underwood and Denley, 1984). A corollary is that the intensity of interspecific interactions should decrease as one approaches a local upper shore limit, because the lower shore species should increasingly suffer from physical stress. A second corollary is that in the absence of the physical stress, a low shore species should be able to exclude a high shore species on the high shore. There are several possible tests of these hypotheses. Connell (1961) transplanted a high shore species below its lower shore limit and showed that it survived in the absence of competitors, but died in the presence of competitors. The reverse experiment, reducing the physical stress and determining the outcome of competition, has not been done.

An earlier paper (Wethey, 1983) gave evidence from field transects that the outcome of competition between the barnacles *Semibalanus* and *Chthamalus* was mediated by heat and/or desiccation stress acting primarily on *Semibalanus*. On transects in Connecticut, *Semibalanus* was found at higher levels on the shore in shaded locations than in sunny areas. The upper shore limit of *Semibalanus* distribution was higher in damp areas than in adjacent dry locations (Wethey, 1983). *Chthamalus* was abundant in areas where *Semibalanus* was absent (Wethey, 1983). In low shore areas from which I removed *Semibalanus, Chthamalus* survived for over a year well below its normal lower intertidal distribution limit (Wethey, 1983 and unpub.).

There is one field experiment that implicated direct sun (rather than emersion) as a limiting factor on *Semibalanus*. Hatton (1938, p. 274) fixed a sun shade several centimeters above a south facing rock surface and noted after 13 months that

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Semibalanus in the experimental shade area had grown bigger than those in direct sun. The growth rates on shaded south-facing sites were indistinguishable from those on north-facing surfaces that were naturally shaded. The effects of heating by the sun were probably more important than drying of the surface, because the experimentally shaded sites dried out at low tide whereas the north facing rocks did not (Hatton, 1938, p. 275). This experiment was unreplicated and had no controls for the effects of the structure of the shade. Hatton did not report on the effect of the experiment on competition between *Semibalanus* and *Chthamalus*.

In this paper I provide experimental evidence for the influence of physical stress on the intensity of competition between two rocky intertidal barnacles. I show that, as I had previously suggested (Wethey, 1983), the intensity of competition is determined on the high shore by physical stress, which primarily affects the dominant competitor.

Materials and Methods

The study was carried out at the Yale University Peabody Museum Field Station, Guilford, Connecticut. Field experiments were established on the south shore of Horse Island, Long Island Sound (41°16′N, 72°45′W). The smooth granite shore has a 15° slope to the southwest. The tidal range is approximately 1.9 meters, and experiments were established at +1.5 m.

Seven treatments were used to test the effects of shade on the distribution and abundance of *Chthamalus* and *Semibalanus*. The treatments were:

1. Unmanipulated site.
2. Two-sided cage (roofless except for mesh, upper and lower shore sides open).
3. Full cage (roofless except for mesh).
4. Two-sided cage with clear plastic roof (upper and lower shore sides open).
5. Full cage with clear plastic roof.
6. Two-sided cage with opaque plastic roof (upper and lower shore sides open).
7. Full cage with opaque plastic roof.

Galvanized steel hardware cloth cages (10 cm l × 10 cm w × 3 cm h, 1.5 cm mesh) were attached with stainless steel screws set in plastic wall anchors in holes drilled in the rock. Roofs of clear Plexiglas were held onto the tops of the cages with the attachment screws. In the shade treatments, the roofs were wrapped with duct tape, making them opaque. Clear roof treatments, roofless treatments, and unmanipulated areas were used as controls for testing the effects of shade and the effects of the presence of a roof. The design was also used to test for the effects of a cage and cage structure. Three replicates of each treatment were established.

Photographs of each of the sites were taken on 14 June 1983 at initiation of the experiment and on 17 July, 10 August, 19 October, and 1 December, 1983. A focal framer on a 3:1 closeup ring provided registration of camera position (Nikonos, 35 mm lens, flash-lit, Panatomic-X film). The number of individuals of each species in each site was counted on enlargements of the photographs. Percent cover was estimated by placing a transparent sheet with 49 uniformly spaced dots over the enlargements. The percent of the dots touching *Semibalanus*, or *Chthamalus* is an estimate of the percent cover of each species (*e.g.*, Menge, 1976; Wethey, 1983). All *Semibalanus* were counted in the percent cover and census measures. Only the *Chthamalus* that were present at the beginning of the experiment were counted. *Semibalanus* settlement had finished before the start of the experiment, but *Chthamalus* larvae settled during the period August to October.

The tests for the effects of shade, and the various controls were made as follows:

1. The control for the presence of an opaque roof is a clear roof. The effects of a roof in the absence of shade were determined by comparing the roofless treatments to the clear roof treatments.

2. The effects of shade in the presence of a roof were tested by comparing the clear roof treatments to the opaque roof treatments.

3. The the control for the presence of a cage is a two-sided cage. The effect of a cage was tested by comparison of the roofless full cages to roofless two-sided cages.

4. The control for the presence of the support structure (wire mesh) was the unmanipulated area. The comparison of unmanipulated areas with two-sided cage treatments is a test of the effect of the presence of the structure.

These tests were all pre-planned contrasts, which were carried out as part of an analysis of variance. Two parameters were tested: change in percent cover of both *Semibalanus* and *Chthamalus*, and percent survival of the two species. Data were transformed by the arcsin transformation prior to analysis to normalize the distributions.

Because all shade and roof treatments had both full cage and two-sided cage supports, it was necessary to test for the effect of the cage before proceeding with the rest of the analysis. If the cage effect is not significant then the remaining pre-planned contrasts can be used. Despite the fact that sums of squares for caged and two-sided treatments are pooled in the shade and roof contrasts, the tests are considered *a priori* because they were all planned in advance (were not suggested by the data), and only a specific limited subset of all possible comparisons was made. The confidence level (*P*-value) only applies to each particular test, not to the whole series of tests, and is only appropriate when the test is pre-planned (*e.g.*, Neter and Wasserman, 1974, p. 472).

If the only important effects are those of sun *versus* shade, then only the shade test should be significant.

Percent cover data were used only to calculate the change in occupation of space between initiation and termination of the experiment. The uniformly spaced dots tended to fall on the same locations on the two samples, making the estimate of absolute change in percent cover more accurate than would be possible with truly spatially independent samples. Because only a difference in percent cover is calculated, the lack of independence does not compromise the analysis. The test of the effect of treatments on changes in percent cover is equivalent to a test of the effect of treatments on survival of a cohort of individuals.

Results

All sites were equivalent in terms of percent cover at the initiation of the experiment (Table I). This means that any differences detected at the end of the experiment are the results of the treatments, not historical effects carried through from initiation.

Population densities of *Semibalanus* were 10.9 (S.D. 3.4) individuals/cm^2 at initiation of the experiment, which was approximately 60 days after settlement (Table I). Densities at settlement were likely to have been much higher than this, since mortality is high in the period soon after settlement (*e.g.*, Connell, 1961; Wethey, 1984).

There were no effects of caging on the survival of *Chthamalus* or *Semibalanus* (Tables II, III). The tests for effect of the structure of the support (two-sided cages *versus* unmanipulated sites) indicated no structure effect (Tables II, III). The experiments were set up at a tidal level above the local upper foraging limit of the primary

TABLE 1

Percent cover of Semibalanus *and* Chthamalus *at initiation on 14 June, 1983*

Semibalanus			
Treatment	Mean	SE	
Roofless	57	5	
Clear Roof	62	5	
Opaque Roof	57	5	
Unmanip	58	7	
Contrast	DF	F	*P*
Roof	1	1.77	0.2047
Shade	1	0.47	0.5042
Cage	1	0.99	0.3356
Structure	1	1.10	·0.3111
MSE = 1490, df = 14			
Chthamalus			
Treatment	Mean	SE	
Roofless	22	5	
Clear Roof	15	5	
Opaque Roof	20	5	
Unmanip	14	7	
Contrast	DF	F	*P*
Roof	1	0.50	0.4927
Shade	1	0.19	0.6723
Cage	1	0.65	0.4352
Structure	1	0.09	0.7685
MSE = 310, df = 14			

Analysis of variance carried out on arcsin-square root transformed percentages. The mean values are transformed back to percents. Abbreviations: DF = degrees of freedom, MSE = mean square error, F = variance ratio, *P* = probability of Type 1 error. Roof contrast is *a priori* comparison of roofless and clear roof treatments. Shade contrast is *a priori* comparison of clear roof and opaque roof treatments. Cage contrast is *a priori* comparison of roofless cages to roofless two-sided cage treatments. Structure contrast is *a priori* comparison of roofless two-sided cages to unmanipulated treatments. Population densities at initiation: *Semibalanus* 10.9/cm^2 (S.D. 3.43), *Chthamalus* 1.3/cm^2 (S.D. 1.06).

predator (*Urosalpinx cinerea*). The cages served primarily to exclude the herbivorous gastropod *Littorina littorea* (mean number per quadrat in July, August, and October samples: cage 0.3, two side 2.1). *Littorina saxatilis* were small enough to enter the cages and were found in abundance at each survey (for example, mean number per quadrat in July samples; cage 27.9, two side 26.9). The primary effect of the roofless and clear roof cages was the growth of a canopy of green filamentous algae from June to October (canopy appeared in 3 of the 6 unshaded cages, percent cover in August 44%, S.D. 33%), and the appearance of a few *Fucus vesiculosus* plants thereafter (*Fucus* appeared in 2 roofless cages, 4 plants in one and 1 plant in the other). The canopy of filamentous green algae evidently did not provide enough shade or water retention to mitigate the effects of sun on *Semibalanus*. Because there was no cage effect on survival of *Semibalanus* or *Chthamalus*, the pre-planned pooling of data from full cages and two sided cages was retained from the tests of the shade and roof effects.

TABLE II

Percent survival of Semibalanus *from June to December*

Treatment	Mean	SE	
Roofless	7	3	
Clear Roof	7	3	
Opaque Roof	21	3	
Unmanip	0	4	
Contrast	DF	F	*P*
Roof	1	0.01	0.906
Shade	1	7.64	0.015
Cage	1	0.21	0.657
Structure	1	1.11	0.309
MSE = 305, df = 14			

Analysis of variance carried out on arcsin-square roof transformed percentages. The mean values are transformed back to percents. Abbreviations and contrasts are as in Table I.

Percent survival of *Semibalanus* was higher in the shade treatments than in the treatments exposed to direct sun (roofless and clear roof) (Table II). Survival was significantly less under the clear roof (7%) than under the opaque roof (21%) (shade effect, Table II). There was no effect of the presence of the roof alone, based on comparison of the clear roof (7% survival) and roofless (7% survival) treatments (roof effect, Table II). Therefore the shade effect is the result of the shade alone and is not confounded by the presence of the structure of the roof.

Percent survival of *Chthamalus* was lower in the shade treatments than in the treatments exposed to direct sun (Table III). Survival under the clear roof (76%) was significantly higher than under the opaque roof (36%) (shade effect, Table III). There was no effect of the presence of the roof alone, based on comparison of the clear roof (76% survival) and roofless (67% survival) treatments (roof effect, Table III). Therefore the shade effect is the result of the shade alone, and is not confounded by the presence of the roof.

TABLE III

Percent survival of Chthamalus *from June to December*

Treatment	Mean	SE	
Roofless	67	12	
Clear Roof	76	12	
Opaque Roof	36	12	
Unmanip	95	17	
Contrast	DF	F	*P*
Roof	1	0.32	0.5805
Shade	1	5.64	0.0324
Cage	1	0.03	0.8611
Structure	1	2.62	0.1278
MSE = 1330, df = 14			

Analysis of variance carried out on arcsin-square root transformed percentages. The mean values are transformed back to percents. Abbreviations and contrasts are as in Table I.

Occupation of space was dramatically affected by the experimental treatments. In the shade treatments *Semibalanus* increased its occupation of space (Table IV) and formed 2.5 cm tall hummocks under the roofs. In the clear roof and roofless treatments, occupation of space by *Semibalanus* decreased (Table IV); any surviving *Semibalanus* were relatively small and no hummocks formed. *Chthamalus* slightly decreased (not statistically significantly) in occupation of space in the shade treatments and remained constant in the clear roof and roofless treatments (Table IV).

The majority of the deaths of *Chthamalus* in the shade treatments were the result of direct interactions with *Semibalanus. Chthamalus* individuals were overgrown, crushed, and undercut by *Semibalanus* (Table V). Individuals that were far enough away from *Semibalanus* that they did not experience direct interference, survived in the shade treatments. Few *Chthamalus* individuals in the sun treatments (roofless and clear roof) were close enough to surviving *Semibalanus* to sustain damage. The *Chthamalus* that were close to *Semibalanus* died as a result of the interaction. There were proportionally very few deaths of *Chthamalus* as a result of unknown causes or of interactions with conspecifics (Table V).

TABLE IV

Changes in space occupation from June to December

Semibalanus			
Treatment	Mean	SE	
Roofless	−34.7	15.4	
Clear Roof	−46.4	15.4	
Opaque Roof	30.4	15.4	
Unmanip	−86.4	21.7	
Contrast	DF	F	*P*
Roof	1	0.08	0.7833
Shade	1	11.38	0.0046
Cage	1	0.35	0.5618
Structure	1	1.21	0.2908
MSE = 2215, df = 14			
Chthamalus			
Treatment	Mean	SE	
Roofless	3.4	10.4	
Clear Roof	0.01	10.4	
Opaque Roof	−25.2	10.4	
Unmanip	26.1	14.7	
Contrast	DF	F	*P*
Roof	1	0.10	0.7623
Shade	1	2.12	0.1674
Cage	1	0.22	0.6468
Structure	1	0.46	0.5075
MSE = 2689, df = 14			

Analysis of variance carried out on arcsine-square root transformed percentages. Mean values transformed back to percents. Values are changes in percent cover from the beginning to the end of the study (positive values indicate an increase in percent cover, negative values indicate a decrease). Abbreviations and contrasts are as in Table I.

TABLE V

Causes of death of Chthamalus

Cause	Shade trtmts. percent	Sun trtmts. percent
Killed by *Semibalanus*		
Overgrown	73	6
Crushed	13	34
Undercut	7	21
Killed by *Semibalanus* and *Chthamalus*		
Crushed	0	2
Killed by *Chthamalus*		
Crushed	0	4
Unknown	6	34

Values are percents of total deaths from particular identifiable causes in the shade and sun treatments. Shade treatments = opaque roof. Sun treatments = clear roof and roofless. Shade treatments: number of individuals = 130, sun treatments: number of individuals = 53.

DISCUSSION

This study examined the influence of physical factors (heat and/or desiccation) on the intensity of interspecific competition between the barnacles *Semibalanus* and *Chthamalus* near the northern geographic limit of *Chthamalus* in New England. In sunny locations the upper shore limit of *Semibalanus* distribution is lower than in more shaded locations and *Chthamalus* survives in areas where *Semibalanus* dies (Wethey, 1983). I argued that the intensity of the competitive interactions between *Chthamalus* and *Semibalanus* were mediated by intolerance of heat and/or desiccation by *Semibalanus* (Wethey, 1983). The experiment described here is a field test of this hypothesis.

The results of the experiment are consistent with the shade/competition hypothesis. In the shade treatments *Semibalanus* survived (Table II) and grew to form hummocks 2.5 cm high. It increased occupation of space at the expense of *Chthamalus* (Tables III, IV, V). In the clear roof and the roofless treatments *Semibalanus* died (Table II) and its occupation of space decreased during the experiment (Table IV). *Chthamalus* remained unchanged in the sun treatments (Tables II, III, IV). No hummocks formed in any of the sun treatments. The results were striking enough that at termination the shade treatments were recognizable from a distance of several meters away on the shore after the hardware was removed.

The controls for the effect of the roof alone and the support structure alone are essential to allow the results of the experiment to be applied to the real world. These controls allow one to separate the effect of shade from the effect of the structure holding the shade above the experimental plots. The clear roof controls were indistinguishable from the roofless treatments, indicating that shade alone was the important factor affecting survival in the shade treatments (Table II). Therefore the results of the experiment can be applied to any locations where shade occurs naturally. The survival of *Semibalanus* is therefore strongly influenced by shade in southern New England.

These results are consistent with the hypothesis that the upper shore limit of *Semibalanus* is set by intolerance of heat and/or desiccation rather than intolerance of emersion. The effect of the shade treatment was similar to that reported by Hatton (1938). He concluded that shade alone strongly influenced growth. Other experiments could not distinguish between the effect of emersion and the effect of heat/desiccation. Hatton (1938) reduced the importance of desiccation and raised the upper shore limit of *Semibalanus* by means of the drips from a slowly draining basin fixed in the high intertidal. Hatton's (1938) drip treatment also may have added food to the experimental individuals (Underwood and Denley, 1984). Foster (1969, 1971a, b) concluded that heat and desiccation were important, based on field and laboratory experiments and observations of changes in the upper shore limit of *Semibalanus* in mid summer (see also Bowman, 1982). Connell (1961b) found that mortality rates measured during hot dry weather were greater than those measured in cooler periods and concluded that desiccation was important. In northern Scotland, *Chthamalus* is more abundant on surfaces that dry out at low tide and *Semibalanus* is more abundant on surfaces that remain wet (Lewis, 1964). *Semibalanus* is more common on north-facing than south-facing shores in the south of England (Crisp and Southward, 1958). As one approaches the southern limit of *Semibalanus,* it become progressively more restricted to shaded locations (Barnes, 1958). The present study provides the first controlled experimental demonstration that shade alone can determine the local upper shore limit.

Underwood and Denley (1984) state that one cannot make the generalization that local upper limits are set by physical stress operating after larval settlement. They erect several alternative hypotheses: animals on the high shore may starve during calm weather because they are not submerged long enough to feed. Alternatively larvae may actively avoid settlement on the high shore. In addition transplant ". . . experiments only reveal sources of mortality of organisms moved outside their normal zone and do not tell us anything definite about reasons for the absence of organisms from such areas" (Underwood and Denley, 1984). The present experiments falsify all of these alternatives posed by Underwood and Denley (1984) and demonstrate that physical stress operating after larval settlement directly limits the upper shore distribution limit of *Semibalanus* in southern New England.

On a local scale the distribution of sun and shade will likely correlate strongly with the distribution of *Semibalanus* and *Chthamalus*, with the latter being prevalent in sunny sites on the high shore (*e.g.*, Wethey, 1983). *Semibalanus* is the dominant competitor and exerts a strong influence on the distribution and abundance of *Chthamalus.* In the treatments where *Semibalanus* survived, it killed neighboring *Chthamalus* individuals by overgrowing, crushing, or undercutting them (Table V). In the absence of *Semibalanus, Chthamalus* survived (Tables II, III, V). Hence the survival of *Semibalanus* to a large extent determines the fate of *Chthamalus* as a result of competition for space. The intensity of competition is in turn determined by the action of heat and desiccation on *Semibalanus.* In sunny sites on the high shore, *Semibalanus* dies and *Chthamalus* experiences little competition (Tables II, III, V). In shaded sites *Semibalanus* survives and *Chthamalus* loses in competition (Tables II, III, V). Thus local zonation is likely the result of postsettlement mortality from interspecific competition in *Chthamalus* rather than the result of any requirements for dry conditions on the part of *Chthamalus* adults or juveniles. These results are consistent with those of Connell (1961) who showed that interspecific competition with *Semibalanus* had a much greater influence on the distribution of *Chthamalus* than did intraspecific competition, or larval settlement pattern.

On a geographic scale, *Chthamalus* is likely to persist only in areas where *Semibalanus* predictably dies on the high shore, providing a refuge from competition (Wethey, 1983). In Massachusetts north of Cape Cod, *Semibalanus* does not die on the high shore (Wethey, 1983), and as a result its upper shore limit does not change during the year. At this location, *Semibalanus* does not settle above the upper shore limit of adults. At Nahant, Massachusetts (north of Cape Cod), I have monitored settlement in sites 10 cm above the upper shore limit of *Semibalanus* and have not seen more than 1 cyprid larva/cm^2 (unpub.). This is in striking contrast to the pattern in Connecticut, where I measured densities of *Semibalanus* metamorphosed spat of 10/cm^2 in June (6 weeks after the end of settlement) at shore levels 20 cm above the upper shore limit of adult distribution (Table I). *Chthamalus* is absent at Nahant and is abundant on the high shore in Connecticut.

On a temporal scale, after a period of hot summers, *Chthamalus* would be expected to increase in abundance, as a result of the lessening of the intensity of competition with *Semibalanus*. After a period of cold summers, *Chthamalus* should decrease as a result of the greater intensity of competition with *Semibalanus*. Such a temporal pattern has been documented by Southward and Crisp (1956), Southward (1967) and Crisp *et al.* (1981) in England. The abundance of *Chthamalus* in southern New England may have increased since the climatic minimum in the early 1800's. The species was noted by Darwin (1854) in collections from Charleston, South Carolina, but not in collections from Delaware Bay or Massachusetts. It was first noted at Woods Hole in 1898 by M. A. Bigelow (Sumner *et al.*, 1913, pp. 191, 646). The first published report was by Sumner (1909). Sumner *et al.* (1913) note "It is hard to believe that this species has been habitually confused with [*Semi*]*balanus balanoides* by the long succession of field naturalists and systematic zoologists who have exploited the shores of New England for over a century. These men erred rather in the direction of discovering too many new species than in ignoring well established ones." Pilsbry (1916) in his monograph on the North American barnacles was equally puzzled by this. Perhaps *Chthamalus* really was rare in the mid 1800's and reinvaded from the south as a result of release from competition with *Semibalanus* brought about by the climatic warming.

The physical environment and biotic interactions combine to determine the dynamics of this high intertidal barnacle assemblage. The intensity of interspecific competition is mediated by physical stress, which primarily affects the dominant competitor. *Semibalanus* can significantly reduce the population densities of *Chthamalus*, even on the high shore, if *Semibalanus* is not killed by physical stress. An understanding of the interplay between physical stress and biotic interactions may allow us to understand not only local zonation, but also geographic limits of species and patterns of long term temporal variation in relation to climatic change.

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LITERATURE CITED

BARNES, H. 1958. Regarding the southern limits of *Balanus balanoides* (L.). *Oikos* **9**: 139–157.

BOWMAN, R. S. 1982. The role of stochastic events in *Balanus/Chthamalus* interactions on Scottish shores. *Abstr. 17th Eur. Mar. Biol. Symp.*

CONNELL, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42**: 710–723.

CONNELL, J. H. 1972. Community interactions on marine rocky intertidal shores. *Ann. Rev. Ecol. Syst.* **3**: 169–172.

CRISP, D. J., AND A. J. SOUTHWARD. 1958. The distribution of intertidal organisms along the coasts of the English Channel. *J. Mar. Biol. Assoc. U. K.* **37**: 157–208.

CRISP, D. J., A. J. SOUTHWARD, AND E. C. SOUTHWARD. 1981. On the distribution of the intertidal barnacles *Chthamalus stellatus, Chthamalus montagui* and *Euraphia depressa*. *J. Mar. Biol. Assoc. U. K.* **61**: 359–380.

DARWIN, C. 1854. *A Monograph on the Sub-class Cirripedia.* Ray Society, London. 684 pp.

FOSTER, B. A. 1969. Tolerance of high temperature by some intertidal barnacles. *Mar. Biol.* **4**: 326–332.

FOSTER, B. A. 1971a. Desiccation as a factor in the intertidal zonation of barnacles. *Mar. Biol.* **8**: 12–29.

FOSTER, B. A. 1971b. On the determinants of the upper limit of intertidal distribution of barnacles (Crustacea: Cirripedia). *J. Anim. Ecol.* **40**: 33–48.

HATTON, H. 1938. Essais de bionomie explicative sur quelques especes intercotidales d'algues et d'animaux. *Ann. Inst. Oceanogr.* **17**: 241–348.

LEWIS, J. R. 1964. *The Ecology of Rocky Shores.* Hodder and Stoughton, London. 323 pp.

MENGE, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecol. Monogr.* **46**: 355–393.

NETER, J., AND W. WASSERMAN. 1974. *Applied Linear Statistical Models.* Irwin, Homewood Illinois. 842 pp.

PILSBRY, H. A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U. S. National Museum; including a monograph of the American species. *Bull. U. S. Nat. Mus.* **93**: 1–366.

SOUTHWARD, A. J. 1967. Recent changes in the abundance of intertidal barnacles in south west England: a possible effect of climatic deterioration. *J. Mar. Biol. Assoc. U. K.* **47**: 81–95.

SOUTHWARD, A. J., AND D. J. CRISP. 1956. Fluctuations in the distribution and abundance of intertidal barnacles. *J. Mar. Biol. Assoc. U. K.* **35**: 211–229.

SUMNER, F. B. 1909. On the occurrence of the littoral barnacle *Chthamalus stellatus* (Poli) at Woods Hole, Mass. *Science* **30**: 373–374.

SUMNER, F. B., R. C. OSBURN, AND L. J. COLE. 1913. A biological survey of the waters of Woods Hole and vicinity. *Bull. U. S. Bureau Fisheries* **31**: 1–794.

UNDERWOOD, A. J., AND E. J. DENLEY. 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. Pp. 151–180 in *Ecological Communities: Conceptual Issues and the Evidence,* D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, eds. Princeton University Press, Princeton.

WETHEY, D. S. 1983. Geographic limits and local zonation: the barnacles *Semibalanus* (*Balanus*) and *Chthamalus* in New England. *Biol. Bull.* **165**: 330–341.

WETHEY, D. S. 1984. Spatial pattern in barnacle settlement: day to day changes during the settlement season. *J. Mar. Biol. Assoc. U. K.* **64**: (in press).